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THE DISTRIBUTION OF VESICULAR-ARBUSCULAR MYCORRHIZAE ON MOUNT ST. HELENS, WASHINGTON

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Abstract

Vesicular-arbuscular mycorrhizae (VAM) occur in most terrestrial ecosystems and are crucial to understanding community structure and function. However, their role in primary succession is poorly understood. This study examined the distribution of VAM propagules, spores, and plants across the Pumice Plains of Mount St. Helens.

VAM colonized plants and propagules were common in sites with thick vegetation, such as areas of relict pre-eruption vegetation and lupine patches, but were very infrequent in barren areas which comprise nearly all of the Pumice Plain. The vegetation of the Pumice Plain is composed primarily of facultatively mycotrophic species which are currently nonmycorrhizal. Mycorrhizal plants occur in refugia and thickly vegetated areas. VAM spore density and richness was low and spores are essentially restricted to densely vegetated habitats.

The focus of this study is the distribution of VAM plants and VAM propagules across the Pumice Plain of Mount St. Helens, and their relationship with microsites. The relationship between VAM and microsites is of interest because microsites are crucial to the colonization dynamics on Mount St. Helens (del Moral and Bliss 1993, Titus 1995).

During primary succession on volcanic substrates, it is unlikely that pioneer species would depend on mycorrhizae (Allen 1991). Only non-host and facultatively mycotrophic species could invade these sites. Obligately mycotrophic species would be prevented from establishing until a population of VAM fungi was present in the soil, presumably having arisen in association with facultatively mycotrophic species. Seral sequences may reflect the mycorrhizal dependence of the colonizing species (Allen 1991). Thus, the pattern of VAM distribution across the primary successional landscape of the Pumice Plain may regulate plant invasion patterns (Allen 1988). However, previous to this study, the distribution of VAM propagules across the Pumice Plain was unknown.

VAM propagules are composed of spores, hyphae and VAM colonized roots. The two indices of VAM density, spore counts and degree of root colonization, are not necessarily correlated (Louis and Lim 1987; Johnson et al. 1991). Spore counts assess only one type of propagule while colonization indirectly estimates all types of propagules. Therefore, root colonization is a more accurate measure of total VAM density. In this study, the distribution of VAM has three facets: 1) The presence of VAM fungal propagules in the soil, i.e., the mycorrhizal inoculum potential (MIP), which is determined through a root bioassay; 2) the presence of VAM plants; and 3) the presence of VAM fungal spores in the soil. This study examines the distribution of these three components of VAM across the Pumice Plain.

Methods

Study site. The Pumice Plain was formed by the 18 May, 1980 eruption of Mount St. Helens (46°12′N, 122°11′W). The Pumice Plain covers 20 km^2 immediately north of the crater between 1150–1300 m elevation. It was formed by the deposit of up to 200 m of material from a debris avalanche, subsequent pyroclastic flows, air-fall pumice, and was repeatedly impacted by later lahars. The Pumice Plain is blanketed by pumice that ranges in depth from 10 to 200 m. The surface is flat or gently sloping, with numerous gullies created by erosion dissecting the surface. Surface pumice particles range in size from 1 mm to 10 cm (del Moral and Bliss 1993).

The climate is maritime, with cool wet winters and warm, dry summers. Periods of drought often occur in July and August. Annual precipitation averages 2373 mm, yet usually less than 5% of this falls between June and August. The growing season begins in June and ends by early September. Temperatures range from mean monthly minima of −4.2°C in January and 7.3°C in August to maxima

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of 0.5°C in January and 22.2°C in July (Spirit Lake Ranger Station (987 m a.s.l.), Pacific Northwest River Basins Commission 1969). Summer temperatures range from 0 to 35°C with a mean ca. 12°C. Surface soil temperatures are often very high in the summer approaching 50°C on tephra surfaces (Reynolds and Bliss 1986).

Pumice Plain soil is immature, with very low concentrations of carbon, nitrogen, and microbial biomass (del Moral and Bliss 1993). Considerable variation in soil moisture values has been recorded between and within microsites. Substrates with fine particles contain more moisture than areas with coarse particles and erosion rills are more moist than other microsites (del Moral and Bliss 1993). In summer the surface tephra dries quickly between rains, thus, most Pumice Plain habitats do not remain moist for periods sufficient to allow seedling establishment. However, the surface layer of tephra acts as a mulch to impede evaporation and is capable of holding considerable moisture at lower depths so that adult plants rarely suffer from drought (Reynolds and Bliss 1986).

Microsites. The seven types of microsites in this study appear to differ in environmental characteristics on the spatial scale of an individual seed or seedling. They were chosen because personal observation and the literature both suggest them to be important to revegetation processes on the Pumice Plain. These sites are:

Flat—sites which have homogeneous gravel, sand or silt substrates in which the topography is level. Pumice particles are less than 5 cm in diameter. Flat sites occupy most of the Pumice Plain and are sparsely vegetated.

Rill—small gullies formed by erosive water action. These are linear habitats that marginally protect seedlings from wind, collect more snow, and have lower solar radiation (del Moral and Bliss 1993). Rill edges are more stable than rill bottoms and drainages.

Near-rock—adjacent to rocks larger than 25 cm in diameter. On exposed surfaces rocks protect seedlings from direct solar exposure, reduce wind and surface temperatures, and are more likely to trap seeds.

Ridges—sites located on small ridgetops where there is evidence of extensive wind erosion.

Lupinus patch—sites associated with dense patches of living and dead *Lupinus lepidus* Douglas. These sites contain higher levels of soil nitrogen and lupines effectively trap seeds and organic matter. *Lupinus* patches are described in Halvorson et al. (1992), del Moral and Bliss (1993), del Moral et al. (1995), Bishop (1996).

Crowded vegetation—sites located in thick vegetation on new volcanically emplaced surfaces which are not dominated by *L. lepidus.*

Refugia—sites with pre-eruption soil exposed by erosion in which some belowground plant organs survived and subsequently sprouted. Refugia are densely vegetated and are confined to the eastern fringe of the Pumice Plain on steep north facing slopes. Refugia vegetation is described by del Moral et al. (1995).

These sites were investigated to determine the distribution of VAM propagules and plants across the Pumice Plain. The first study looks at the distribution of VAM propagules, the second at the distribution of VAM plants and the third at the distribution of VAM spores.

Corn bioassay for assessing VAM propagule distribution. Soil samples were collected at 20 representative locations within each site (except refugia) in July 1991. Four 250 g samples from the upper 8 cm of soil were collected at each location and combined to form two composite samples. Soil was sifted to remove all particles larger than 4 mm, amended with 20% sterile perlite to increase porosity, and 650 g was placed into 10 cm by 10 cm freely draining plastic pots. Bioassays were conducted with non-fungicide treated *Zea mays* seeds. All pots were watered daily with tap water. Fertilizer was applied in 50 ml aliquots per pot of Colwell's solution minus phosphorus at planting and at weekly intervals throughout the experiment. Colwell's solution mimics natural proportions of nutrients in typical temperate soils (Colwell 1943; R. B. Walker personal communication). The control consisted of 20 pots of sterile greenhouse soil placed randomly among the treatment pots and planted with corn to determine if contamination by greenhouse VAM propagules occurred. Previous work showed that VAM propagules, if present, rapidly colonize corn in the greenhouse (Titus personal observation). Pots were randomized and maintained at the University of Washington Botany Greenhouse at 20–25°C, and rotated every 10 days. Bioassay plants were grown for 35 days from 20 July to 14 August 1991. Plants were harvested, roots washed, and frozen at −18°C until October 1991 at which time roots were assayed for VAM colonization. The quantity of inoculum in the soil, mycorrhizal inoculum potential (MIP), was estimated by percent colonization of corn roots (Moorman and Reeves 1979; Doerr et al. 1984; Johnson and McGraw 1988).

Staining. Roots were washed, cleared and stained with trypan blue (Brundrett et al. 1994; E. Cázares, Oregon State University, personal communication). Percent colonization was estimated by placing a grid of 1 cm squares below a petri plate which contained the root sample under a dissecting microscope. One hundred locations where a root crossed a line on the grid were scored for mycorrhizae. Many samples were examined under higher power to ascertain that the fungus was indeed VAM. Root segments containing vesicles, arbuscles or intercellular hyphal coils or hyphae were recorded as being colonized. The number of mycorrhizal "hits" is an

estimate of the percent of the root colonized (Brundrett et al. 1994).

Mycorrhizal colonization of pioneer species. The roots of 14 plants of six major pioneer species were collected from each of the seven site types at different locations across the Pumice Plain. Most root samples were collected during July, 1992, and the remainder during July, 1993. All sampled plants were at least 4 m from their nearest neighbor, except for those in lupine patches, crowded vegetation and refugia. Species sampled were *Anaphalis margaritacea* (L.) Benth. & Hook., *Carex mertensii* Prescott, *Epilobium angustifolium* L. ssp. *circumvagum* Mosq., *Hieracium albiflorum* Hook., *Hypochaeris radicata* L. and *Penstemon cardwellii.* In addition to these target species, roots were collected from several other naturally occurring species where they occurred. Roots of these species were not collected in all microsite types because they only occurred in certain ones. Roots were washed when harvested and stored in alcohol until they were cleared and stained to assess VAM colonization as above.

Spore isolation. Soil samples were collected using two sampling regimes. For the first regime soil was collected from 20 representatives of each of the seven site types. Four 100 ml soil samples were collected from the top 8 cm of soil and combined to form a single sample during August 1993.

The second sampling regime was part of a larger study. Percent cover of each plant species in 150 100 m^2 circular plots was assessed across the Pumice Plain during summer, 1993. Vegetation of these plots were grouped into five habitat types based on substrate and vegetation (del Moral et al. 1995). In conjunction with vegetation sampling, 100 ml of soil were collected at each of four locations within each plot and combined into a single sample.

Soil samples were dried at room temperature and stored at 3°C in sealed plastic bags. Spores were extracted from two subsamples of the soil from each plot by the wet-sieving and decanting technique (Gerdemann and Nicolson 1963; Pacioni 1992; Brundrett et al. 1994). One hundred and fifty ml of soil were placed into a 1.651 mm mesh sieve above 0.417 and 0.052 mm mesh sieves. The soil was washed vigorously with water. Roots in the top sieve and soil from the fine mesh bottom sieve were examined in a petri dish under a dissecting microscope at 40× power for VAM spores.

In order to compare spore extraction techniques, the soil from ten samples with two replicates each were analyzed using both the wet-sieving with decanting technique and the differential water/sucrose centrifugation method (Ianson and Allen 1986). Selected soil samples were those likely to contain VAM spores. Spore isolation efficiency was not improved using the differential water/sucrose technique. Although Ianson and Allen (1986) found better spore isolation with the differential water/sucrose technique, the extremely low organic matter content of Pumice Plain soils obviated the need for improved resolution in the case of these soils.

Table 1. VAM Corn Bioassay for the Determination of Mycorrhizal Inoculum Potential (MIP) of Pumice Plain Soil. Soil MIP is shown by percent VAM colonization of corn roots. % plants colonized is the percentage of the plants of each species which were colonized by VAM. (mean ± standard deviation, n = 20 paired samples).

Microsite	MIP	% plants colonized
Flat	0	0
Near Rock	0	0
Ridge	0	0
Rill	0.3 ± 0.6	15
Lupine Patch	3.0 ± 3.3	60
Crowded Vegetation	4.3 ± 3.0	70

Spores were isolated and stored dry on filter paper. Spore types were determined from the experience of the third author and the use of spore identification guides (Mosse and Bowen 1968; Gerdemann and Trappe 1974; Trappe 1982; Morton 1988; Schenck and Perez 1990).

Data analysis. Mean percent mycorrhizal colonization was determined to yield MIP (Experiment I) and mean colonization (Experiment II). In Experiment III, spore density was averaged and richness determined for each site and for each habitat type. The preponderance of zeros precluded statistical data analysis, so values are reported only as observational data. Although both parametric and non-parametric techniques are robust for violations of their respective assumptions, the statistical techniques appropriate for analysis of this experimental design (e.g., one-way ANOVA or the Kruskal-Wallace test (Zar 1984)) are invalid for the analysis of data with many zeros. Even non-parametric statistics require homoscedastic variances. This aside, the patterns in the data are clearly apparent without statistical tests. Frequency of VAM colonization or spores are also reported.

Results

Corn bioassay for assessing VAM propagule distribution. Ridge, flat, and near-rock substrates contained no detectable MIP. Rill microsites occasionally contained VAM propagules, whereas lupine patch and densely vegetated site soils usually contained mycorrhizal inoculum (Table 1).

Mycorrhizal colonization of pioneer species. Anaphalis margaritacea, Hieracium albiflorum and *Hypochaeris radicata* were without mycorrhizal colonization in flat, ridge and near-rock sites, but were mycorrhizal in rill, lupine patch, crowded vegetation and refugia (Table 2). *Carex mertensii* was without mycorrhizal colonization in all sites,

TABLE 2. VAM COLONIZATION OF PLANT SPECIES COLLECTED FROM MICROSITES ON THE PUMICE PLAIN. (mean ± standard deviation, n = 14). Flat, ridge and near rock microsites contained no VAM plants and are not shown.

	Microsite							
	Rill		Lupine patch		Crowded vegetation		Refugia	
Species	% VAM colonization	% plants colonized	% VAM colonization	% plants colonized	% VAM colonization	% plants colonized	% VAM colonization	% plants colonized
Anaphalis margaritacea	1.1 ± 2.6	36	8.3 ± 15.3	57	10.2 ± 12.6	86	6.4 ± 7.8	63
Carex mertensii	0	0	0	0	0	0	0.1 ± 0.4	14
Epilobium angustifolium	0	0	2.0 ± 5.6	29	0.4 ± 1.6	14	4.2 ± 6.6	36
Hieracium albiflorum	0.2 ± 0.8	14	4.9 ± 9.3	64	5.3 ± 12.3	64	8.9 ± 10.5	50
Hypochaeris radicata	0.9 ± 2.5	29	8.1 ± 11.8	64	8.0 ± 15.5	33	10.7 ± 13.7	50
Penstemon cardwellii	0.8 ± 2.8	7	3.2 ± 4.2	43	7.0 ± 7.8	79	15.7 ± 9.0	79

except for a trace of VAM in refugia. *Epilobium angustifolium* was not colonized in rill microsites, but was occasionally colonized in lupine patch, crowded vegetation and refugia. The species with the highest mycorrhizal colonization was *A. margaritacea,* and the site with the most VAM plants was crowded vegetation. Most of the VAM fungal hyphae observed were of the fine endophyte type. Non-target species were all nonmycorrhizal in flat, ridge and near-rock sites (Table 3). Only *Juncus parryi* Engelm. was mycorrhizal in rill microsites. *Juncus parryi* and *Lupinus lepidus* were mycorrhizal in lupine patches. Many species were mycorrhizal in crowded sites and refugia, and species restricted to refugia were usually mycorrhizal.

Spore distribution. No spores were found in flat, rill, or near-rock sites. Densities were variable where spores were found in dead lupine, crowded vegetation, and refugia (Table 4). Dead lupine and crowded vegetation microsites with VAM spores often were located far from refugia. Most refugia samples contained many spores.

Pumice barrens, pyroclastic surfaces and drainages (del Moral et al. 1995) rarely contained VAM fungal spores (Table 5). Samples containing spores were usually located near refugia. The only exception was an isolated barren pumice site which also contained a large willow. Lupine patches occasionally contained spores which, when present, were in high densities. Lupine patches which contained spores were widely spread across the Pumice Plain. Refugia almost always contained spores.

Three spore types were found: *Glomus macrocarpum* (Tul. and Tul.), *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe, and an *Acaulospora* type. The most common spores found were dead (which are empty), dark brown, brassy, or black. There was usually only one spore type present in a sample (not including dead spores which were usually present), however, all three spore types occurred in microsites and habitat types where spores were common.

DISCUSSION

VAM distribution. Based on observational data only, microsites differ in MIP and spore density, and pioneer species differ in mycorrhizal colonization depending on the microsite it inhabits. Sites with thicker vegetation contained more VAM propagules and VAM plants.

After the 1980 eruption, the Pumice Plain was free of VAM fungal propagules (Allen 1987). The VAM propagules detected in this study show that dispersal forces, most likely animals (Allen 1987), have been returning VAM propagules to this landscape. The invasion of VAM propagules is sporadic as some microsites contain more mycorrhizal propagules and more heavily colonized plants than do other microsites. This supports the patch-dynamic model which proposes that the pattern of VAM fungal propagules dispersed by animals searching among patches for food and cover in sparsely vegetated landscapes creates a patchy distribution of inoculum (Allen 1987, 1988). This patchiness may also result from the ability of certain microsites to effectively trap windborne or waterborne propagules.

VAM spores were uncommon across the Pumice Plain, but they are present in crowded and lupine patch microsites. The bulk of the Pumice Plain appears to remain VAM spore free. Evidence for a non-patchy landscape level spread of VAM fungi was observed in the plots adjacent to refugia in which VAM propagules were found. Since refugia are on steep slopes, VAM propagules could immigrate to adjacent barren and drainage habitats by erosion. Plant diversity is also slightly higher in areas adjacent to refugia (del Moral et al. 1995). However, one pumice barren plot distant from sites with high levels of VAM spores contained VAM spores. This is evidence for a patchy distribution of VAM spores and adds support to the patch-dynamic model (Allen 1988). This pumice barren site contained a large willow which is probably a locus for small mammal activity in a barren landscape. In

TABLE 3. VAM COLONIZATION OF PLANT SPECIES COLLECTED FROM MICROSITES ON THE PUMICE PLAIN. n = sample size. (mean ± standard deviation).

	Microsite								
	Flat			Ridge			Near rock		
Species	n	% VAM colonization	% plants colonized	n	% VAM colonization	% plants colonized	n	% VAM colonization	% plants colonized
Achillea millefolium									
Agrostis pallens	4	0	0	2	0	0	4	0	0
Agrostis scabra	7	2.3 ± 6.1	14	2	0	0	7	0	0
Blechnum spicant									
Calyptridium umbellatum	4	0	0				3	0	0
Carex pachystachya	3	0	0	3	0	0	3	0	0
Carex phaeocephala	3	0	0	3	0	0	3	0	0
Cirsium arvense							2	0	0
Epilobium anagallidifolium	5	0	0	2	0	0	4	0	0
Epilobium brachycarpum									
Epilobium ciliatum									
Eriogonum pyrolifolium									
Fragaria virginiana									
Gnaphalium uliginosum									
Juncus mertensianus									
Juncus parryi	10	0	0				2	0	0
Luetkea pectinata									
Lupinus latifolius	4	0	0				4	0	0
Lupinus lepidus	17	0	0	6	0	0	16	0	0
Luzula parviflora									
Phacelia hastata									
Polygonum minimum									
Ribes laxiflorum									
Rubus lasiococcus									
Rubus spectabilis									
Saxifraga ferruginea	5	0	0				4	0	0
Sambucus racemosa									
Senecio sylvaticus	8	0	0	4	0	0	6	0.7 ± 1.6	17
Smilicina racemosa									
Spergularia rubra	2	0	0	0	0	0	2	0	0
Vaccinium membranaceum									
Vancouveria hexandra									

addition, several of the crowded vegetation and lupine patch microsites which contained VAM spores were isolated across the Pumice Plain far from refugia, adding further support to the patch-dynamic model. The differences in spore counts for lupine patch and refugia between Tables 4 and 5 were not unexpected due to the large standard deviations and patchy nature of spore distribution (Anderson et al. 1983; St. John and Koske 1988).

Mycotrophic Status of Colonizing Species

Glomus tenuis. Glomus tenuis (Greenall) Hall is distinguished by hyphal diameters in the 0.5–1.5 μm range (Hall 1987). Other *Glomus* species have coarse (5–30 μm in diameter) hyphae (McGonigle and Fitter 1990; Wang et al. 1993). Therefore, only root colonizations caused by *G. tenuis* can be identified confidently in the absence of sporulating structures (Carling and Brown 1982; Hall 1987). Colonization by *G. tenuis* has been found to be highest in dry very low phosphorus environments (Rabatin 1979), low pH soils (Wang et al. 1993), and in alpine environments (Read and Haselwandter 1981; Mullen and Schmidt 1993). *Glomus tenuis* is also often the dominant VAM fungal species in pioneer species and disturbed environments (Daft and Nicolson 1974). In this study, fine endophyte hyphae were observed frequently, but no spores of *G. tenuis* were detected. *Glomus tenuis* spores may be too small (7–12 μm) to be extracted by the wet sieving technique (Hall 1987; Wang et al. 1993). Thus the possibility exists that these spores are common but were not detected. Although spores are the only way to identify *Glomus* species, they are not indicative of the actual infectivity of a soil and should be used only in conjunction with other indices. For example, no spores were detected in rill microsites, but there was some VAM colonization of corn roots and the target species in rills were occasionally VAM.

Table 3. Extended

Microsite								
Rill			Lupine patch			Crowded vegetation		
n	% VAM colonization	% plants colonized	n	% VAM colonization	% plants colonized	n	% VAM colonization	% plants colonnized
						2	6	100
4	0	0	4	0	0	12	8.0 ± 21.8	25
7	0	0	7	0	0	6	0.4 ± 0.9	17
2	0	0	1	0	0			
3	0	0	3	0	0	5	0	0
3	0	0	3	0	0	5	0	0
3	0	0	2	0	0	3	5.7 ± 4.0	100
			4	0	0	2	0	0
2	0	0				2	15.0 ± 7.1	100
						2	0	0
						1	0	0
						6	0	0
11	0.5 ± 1.5	9	8	9.0 ± 7.0	88	16	0.8 ± 2.6	13
1	0	0						
						5	0	0
16	0	11	19	0.2 ± 0.6	11	6	0.7 ± 1.6	77
						14	0	0
						2	4.0 ± 5.7	50
						2	0	0
5	0	0	1	0	0	2	1.0 ± 1.4	50
4	0	0	5	0	0	4	1.5 ± 1.9	50
2	0	0				0	0	0

Carex spp. are considered to be non-hosts (Powell 1975; Anderson et al. 1984), although mycorrhizal *Carex* spp. have been found in the alpine (Read and Haselwandter 1981; Allen et al. 1987) and in grasslands (Read et al. 1976). VAM *Carex mertensii* plants were only observed in two individuals in this study. *Juncus parryi* is generally thought to be in a non-host genus (Powell 1975). However, in this case it was heavily colonized by VAM in rill, lupine patch and crowded sites. Genera-wide generalizations of mycorrhizal dependence may be inaccurate and extensive examinations of the species must be conducted to ascertain mycotrophy (Read et al. 1976; Newman and Reddell 1987).

Annuals are often considered to be non-hosts (Trappe 1987; Boerner 1992; Peat and Fitter 1993), but in this survey *Senecio sylvaticus* was frequently mycorrhizal. Allen et al. (1992) found the annual *Epilobium paniculatum* to be mycorrhizal in a lupine patch. In this survey the species was found to be nonmycorrhizal.

Allen et al. (1992) found *Lupinus latifolius* J. Agardh. and *L. lepidus* to be mycorrhizal, while this survey found *L. lepidus,* but not *L. latifolius,* to be mycorrhizal. Avio et al. (1990) observed *Lupinus* to be a strongly non-host genus. O'Dell and Trappe (1992) found both *L. lepidus* and *L. latifolius* to be occasionally mycorrhizal. They located a mycorrhizal *L. latifolius* on Mount St. Helens but did not find a mycorrhizal *L. lepidus* on the volcano. O'Dell and Trappe (1992) suggested that VAM fungi may need to be established on a companion host before colonizing roots of lupines.

Most plant species now colonizing Mount St. Helens barren sites appear to be facultatively mycotrophic (Titus 1995). This status supports a broad range of tolerance to VAM, from rarely mycorrhizal to nearly always colonized depending upon the species, neighboring species and site conditions (Allen 1991; Boerner 1992).

VAM fungal species. VAM fungal richness was low, with only three spore types, but greater than the single species (*Glomus macrocarpum*) found in the blast zone by Allen et al. (1984), Allen and

TABLE 3. CONTINUED

Species	Microsite: Refugia n	% VAM colonization	% plants colonized
Achillea millefolium			
Agrostis pallens			
Agrostis scabra			
Blechnum spicant	2	5.0 ± 0	100
Calyptridium umbellatum			
Carex pachystachya			
Carex phaeocephala			
Cirsium arvense			
Epilobium anagallidifolium			
Epilobium brachycarpum			
Epilobium ciliatum			
Eriogonum pyrolifolium			
Fragaria virginiana	3	8.3 ± 13.6	67
Gnaphalium uliginosum			
Juncus mertensianus			
Juncus parryi	0	0.5 ± 1.5	9
Luetkea pectinata	4	0	0
Lupinus latifolius			
Lupinus lepidus			
Luzula parviflora			
Phacelia hastata			
Polygonum minimum			
Ribes laxiflorum	4	15.0 ± 9.1	100
Rubus lasiococcus	2	0	0
Rubus spectabilis	4	16.0 ± 5.9	100
Saxifraga ferruginea			
Sambucus racemosa	4	20.0 ± 12.8	100
Senecio sylvaticus	2	4.0 ± 2.8	100
Smilicina racemosa	4	30.0 ± 14.1	100
Spergularia rubra			
Vaccinium membranaceum	4	25.0 ± 7.7	100
Vancouveria hexandra	2	0	0

MacMahon (1988), and Allen et al. (1992). This indicates that VAM fungal species are invading the blast zone or at least proliferating into detectable densities. The preponderance of inviable spores found in this study is not unusual (Read et al. 1976;

TABLE 4. NUMBER AND RICHNESS OF VAM FUNGAL SPORES IN 150 ML SOIL SAMPLES FROM MICROSITES ON THE PUMICE PLAIN. (mean ± standard deviation for spore counts, n = 20 for each microsite type). [1] Mean richness is based only on samples which contained spores.

Microsite	Mean number of spores	% samples with spores	Mean richness[1]
Flat	0	0	—
Near Rock	0	0	—
Ridge	0	0	—
Rill	0	0	—
Lupine Patch	13.6 ± 29.2	55	1.4
Crowded Vegetation	18.4 ± 41.1	70	1.3
Refugia	20.7 ± 49.6	85	1.8

Berliner and Torrey 1989). The patchy nature of VAM species distribution is evidenced by the large variance in spore densities and by the presence of different spore types in different sites with little overlap. However, each species was present in the microsites and habitat types which had detectable spore populations. It is important to note the difference in sampling intensity between above- and belowground environments. Plot size in del Moral et al. (1995) was 100 m^2, where as the surface area of the belowground sampling effort was only approximately 400 cm^2, which is 0.0004 as large as the aboveground sampling area. Therefore, statements about patchy spore distributions must be regarded in the light of the small belowground sampling area (Anderson et al. 1983). In the few studies which address VAM species distribution, richness is usually low and density variable. It is therefore difficult to draw conclusions about successional patterns in VAM fungal types from the results presented here.

CONCLUSION

This study assessed both VAM colonization and VAM fungal propagules. The results are comple-

TABLE 5. NUMBER AND RICHNESS OF VAM FUNGAL SPORES IN 150 ML SOIL SAMPLES FROM HABITAT TYPES ON THE PUMICE PLAIN. Habitat types based on del Moral et al. (1995). "Near" indicates a site adjacent to a refugia, "far" indicates a site distant from a refugia. n = sample size. (mean ± standard deviation for spore counts). [1] Mean richness is based only on samples which contained spores.

Habitat type	n	Mean number of spores	% samples with spores	Mean richness[1]
Pumice Barrens–near	11	1.5 ± 3.0	4	1
Pumice Barrens–far	32	0.03 ± 0.2	3	1
Pyroclastic Surfaces	15	0	0	—
Drainages–near	4	0.3 ± 0.5	25	1
Drainages–far	15	0	0	—
Wetlands	23	0	0	—
Lupine Patches	16	10.5 ± 26.2	25	1.5
Refugia	26	14.5 ± 33.1	62	1.3

mentary and converge to the conclusion that the Pumice Plain remains essentially VAM free, except for the few isolated lupine patch and crowded sites. Refugia contain VAM fungal propagules and mycorrhizal plants. The sparse vegetation of the Pumice Plain is composed largely of facultatively mycotrophic species which are at present nonmycorrhizal.

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